Predation risk drives the expression of mobbing across bird species

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Abstract: Many species approach predators to harass and drive them away, even though mobbing a predator can be deadly. However, not all species display this behavior, and those that do can exhibit different behaviors while mobbing different predators. Here we experimentally assessed the role of social and ecological traits on the expression of mobbing behavior in a bird community in SE Brazil (n = 157 species). We exposed birds to models of two morphologically similar diurnal owls that pose different risks, and assessed which species engaged in mobbing. Among those that mobbed, we evaluated how they adjusted their mobbing behavior depending on the predator type. We tested the hypothesis that only species that are at risk and can afford to mob engage in this antipredator behavior. We found that species that engaged in mobbing are in the body mass range of potential prey, forage in the understory or in the canopy, and form flocks. A species' social system did not influence its mobbing behavior. Furthermore, species that engaged in mobbing formed larger mobbing assemblages when facing a high-risk predator, but mobbed more intensely when facing a low-risk predator. Our findings support our predictions, namely that the expression of mobbing is limited by its costs.

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Running title: Risks limit mobbing in birds

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Abstract

Many species approach predators to harass and drive them away, even though mobbing a predator can be deadly. However, not all species display this behavior, and those that do can exhibit different behaviors while mobbing different predators. Here we experimentally assessed the role of social and ecological traits on the expression of mobbing behavior in a bird community in SE Brazil (n=157 species). We exposed birds to models of two morphologically similar diurnal owls that pose different risks, and assessed which species engaged in mobbing. Among those that mobbed, we evaluated how they adjusted their mobbing behavior depending on the predator type. We tested the hypothesis that only species that are at risk and can afford to mob engage in this anti-predator behavior. We found that species that engaged in mobbing are in the body mass range of potential prey, forage in the understory or in the canopy, and form flocks. A species' social system did not influence its mobbing behavior. Furthermore, species that engaged in mobbing formed larger mobbing assemblages when facing a high-risk predator, but mobbed more intensely when facing a low-risk predator. Our findings support our predictions, namely that the expression of mobbing is limited by its costs.

Keywords: mobbing, birds, prey-predator interaction, anti-predator behavior, predation risk.

Introduction

Predation is an important selective force, facilitating the evolution of anti-predatory adaptations, such as mobbing behavior. During mobbing, potential prey approach a potential predator to harass and sometimes even attack it, with the primary function of driving the predator away (Curio et al. 1978a; Caro 2005). Thus, mobbing is likely to be adaptive (Curio et al. 1978a; Vieth et al. 1980), reducing the immediate risk for the mobber (Pavey and Smyth 1998). Moreover, moving-on a predator may limit the future risk of attacks (Flasskamp 1994). However, mobbing can be costly since predators may kill prey during mobbing (Sordahl 1990; Motta-Junior 2007).

A large number of field studies investigated the costs and benefits of mobbing in single species, showing that this behavior can increase the chances of survival for the mobber, their offspring, and their relatives (Shields 1984; Pavey and Smyth 1998; Griesser and Suzuki 2017). Also, mobbing can serve as an opportunity to recruit partners for future mobbing events (Krams et al. 2008). Generally, it is expected that the costs and benefits of mobbing vary across species, influencing its expression (Dugatkin and Godin 1992; Pavey and Smyth 1998; Krama and Krams 2005). However, we lack comparative studies that investigate the influence of ecological and social traits on the expression of mobbing across species, and how these factors influence this behavior depending on the risk posed by a predator. Accordingly, it remains unclear why only some species but not others engage in mobbing when encountering certain predators.

87

88 Here we take a comparative, phylogenetically-controlled approach to assess
89 correlates of mobbing behavior in birds. We exposed a bird community in SE
90 Brazil to models of two diurnal perch-hunting owls that differ in their risk. We
91 examined which social and ecological traits are associated with engagement in
92 mobbing, testing four non-exclusive hypotheses:

93 i) *Size matters hypothesis*: We predicted that only species that are
94 potential prey should engage in mobbing. Predators can only kill prey of a given
95 body size (Valcu et al 2014), and thus only species that fall within the size range
96 of potential prey should engage in mobbing.

97 ii) *Safe niche hypothesis*: We predicted that ground-dwelling species
98 should be less likely to mob perch-hunting owls than species that forage in the
99 understory or canopy. Ground-dwelling species are more vulnerable to perch-
100 hunting predators with a top-down hunting strategy (Ekman 1986; Suhonen
101 1993), as they are more easily killed by these predators and have less
102 possibilities to escape in case of an attack.

103 iii) *Safety in numbers hypothesis*: We predicted that being in a group
104 minimizes the per capita risk of being killed (Hamilton 1971, Hogan et al. 2017).
105 Thus, solitary species are less likely to mob than group-living and flocking
106 species due to the higher risk during mobbing.

107 iv) *Social facilitation hypothesis*: We predicted that mobbing may provide
108 a social learning opportunity to recognize predators (Curio et al. 1978b) for
109 family members (Griesser and Suzuki 2016, Griesser and Suzuki 2017). Thus,

family living species (including cooperative breeders; Griesser et al. 2017) are predicted to mob more than non-family living species.

Furthermore, among the species that do engage in mobbing, we tested the 'mobbing plasticity hypothesis', which predicts that birds can recognize the risk posed by predators (Caro 2005) and adjust their mobbing behavior accordingly. Thus, species that engage in mobbing are predicted to mob a more dangerous predator more intensely and in larger mobbing assemblages. Moreover, since mobbing can be used as nest defense (Arnold 2000) we predicted that birds would mob more intensely during the breeding season than during the non-breeding season (Shedd 1982; Shedd 1983).

Methods

This study was carried out on Cauaia Ranch, Minas Gerais State, SE Brazil (19°28`S 44°01`W) between February 2011 and February 2012. The study site is part of the Environmental Protection Area Carste Lagoa Santa, where semi-deciduous forests and Brazilian savannah patches dominate the landscape, forming a mosaic of pastures, marshes, deciduous forests and temporary lagoons.

We exposed the local bird community to models of two diurnal owl species that are morphologically similar but differ in their risk to birds: a Ferruginous Pygmy-owl (*Glaucidium brasilianum*) that represents a high risk predator, i.e., 43% of its diet consists of birds (Carrera et al. 2008), and a Burrowing Owl (*Athene cunicularia*) that represents a low-risk predator, i.e.,

95% of its diet consists of arthropods (Zilio 2006), but occasionally eats birds (Motta-Junior 2006). Both owls have a preference for small-sized prey: Ferruginous Pygmy-owls hunt prey weighing on average 43.7 g (min-max: 12.5-225.0 g) (Carrera et al. 2008), and Burrowing Owls hunt prey weighing on average 39.2 g (min-max: 0.07-210 g, with 60% of their diet composed of prey weighting 0.07 to 20 g) (Nabte et al. 2008).

We chose 18 experimental locations that were at least 250 m apart to reduce the risk of resampling the same individuals on the same day (Bibby et al. 2012). In each location, we performed 5-6 experiments per model following a Latin square design, resulting in 96 experiments per model. For each experiment, we selected a different location in a relatively open area on the forest edge. We placed the predator model on a 1.5 m high pole, 2 m away from an approximately 3 m high tree. We attached marks at 2, 5, 10 and 15 m in all four cardinal directions from the model, facilitating the assessment of the distance between mobbers and the model. Experimental locations were selected to allow the observer good visibility of at least 20 m in all directions around the model.

We placed a speaker on the ground below the model to playback vocalizations of the model species (30 sec calls, 15 sec silence, during 10 min) to simulate the presence of a live predator. During the experiment, an observer was positioned 10-15 m away from the model wearing camouflage clothing. We recorded the behaviors and distance to the predator model of all present

158 individuals. All trials were conducted between 06h00 and 12h00 local time,
159 corresponding to the time of the day with the highest activity of birds. No trials
160 were conducted on rainy days.
161
162 We recorded all species observed in the experimental locations three
163 minutes before each experiment (576 minutes of observation) to assess the
164 bird species present in the study site. We also included all species that mobbed
165 the models during the trials (1920 minutes of observation).
166
167 We obtained data on the body mass, diet, foraging strata, flocking
168 behavior and social system of the species from handbooks (del Hoyo et al.
169 2015). Species were categorized according to their foraging strata: ground,
170 understory or canopy; their flocking habits: species that live in stable group or
171 joins flocks, or solitary species; and to their social system: non-family living,
172 family-living (offspring delay dispersal >50 days beyond independence
173 (Drobniak et al. 2015)), or cooperatively breeding species (Cockburn 2006).
174 Species whose social system is unknown were not considered for the analysis
175 including this variable.
176
177 We assigned the mobbing status of a species based on the response in
178 all experiments using a categorical variable with two levels: i) mobber: a species
179 that mobbed during at least one experiment; ii) non-mobber: a species that is
180 present at the study site but was never observed mobbing).
181

We assessed the mobbing intensity of all individuals that engaged in mobbing on an increasing ordinal scale from 1-7 (adapted from (Chandler and Rose 1988; Motta-Junior and Santos-Filho 2012)). Mobbing intensity was ranked based on the mobber's distance from the model (in meters), and its behavior (emitting calls or not, and/or visual displays such as flapping wings, rattling the tail feathers, ruffling the crown feathers and/or repetitive movements with wings, tail or head): 1) an individual was > 10 m away from model making visual displays and/or giving warning calls or being silent, 2) an individual was ≤ 10 m and > 5 m away making visual displays and/or giving warning calls or being silent, 3) an individual was ≤ 5 m and > 2 m away being silent, 4) an individual was ≤ 5 m and > 2 m away making visual displays and/or giving warning calls, 5) an individual was ≤ 2 m away being silent, 6) an individual was ≤ 2 m away making visual displays and/or giving warning calls but not attacking the model, and 7) an individual was physically attacking the model.

Statistical Analyses

We used the software R 3.3.2 for the statistical analyses (R Core Team 2016), using Generalized Linear Mixed Models in the package MCMCglmm (Hadfield 2010). This method allowed us to perform phylogenetic regression analyses (Ives and Garland 2014) of response variables that do not follow a Gaussian error distribution. To test our hypotheses we ran three separate models to assess the influence of independent factors on i) whether species mob or not (mobbers vs non-mobbers, categorical variable with two levels), ii) the mobbing intensity (an ordinal scale (rank scale 1-7, see above), and iii) the mobbing

206 assemblage size (a discrete numerical variable). The 'MCMCglmm' statistical
207 R package uses Markov chain Monte Carlo (MCMC) probabilistic sampling
208 technique, making the analysis of complex models possible (Hadfield 2012).
209 Furthermore, the use of 'MCMCglmm' allowed us to include random variables
210 in the models, and to control for the influence of phylogeny (Hadfield 2012; Ives
211 and Garland 2014).
212
213 We included a consensus tree at the species level of a recent phyla-wide
214 avian phylogeny (Jetz et al. 2012) as a random effect to control for phylogenetic
215 non-independence. The MCMCglmm models were run for 100,000 iterations,
216 with a 1,000 burn-in period and samples drawn every 100 iterations. Our
217 models resulted in comparable effective sample sizes for all factors (~1000),
218 and visual inspection of trace plots indicated proper mixing of the models.
219
220 To test the four hypotheses regarding the influence of ecological and
221 social traits on whether or not species engage in mobbing behavior, we
222 included the following species-specific explanatory variables into the model:
223 body mass (log-transformed, in grams), foraging strata, flocking habits, social
224 system. We also included the encounter rate per minute as a covariate to
225 control for the influence of relative species abundance. We used a categorical
226 mixed model using the logit link function in MCMCglmm. For this model we
227 excluded species for which the social system is unknown. Thus, the analysis
228 was conducted with a reduced dataset of 145 species, of which 67 species
229 mobbed.

Within the species that mobbed, we assessed the factors that influenced mobbing assemblage size and mobbing intensity with separate models. For the former, we performed a phylogenetically-controlled Poisson-distributed generalized linear mixed model with log link, using MCMCglmm. We included the following explanatory variables in this model: predator model (high-risk, low-risk), season (breeding season (September to February), non-breeding season (March to August)), and the maximum mobbing intensity during an experiment of each individual (ordinal scale from 1 to 7). To test mobbing intensity we performed a phylogenetically-controlled ordinal generalized linear mixed model with a probit function, using MCMCglmm. We included the maximum mobbing intensity of each individual as the response variable and the following explanatory variables: predator model (high-risk, low-risk), season (breeding season (September to February), non-breeding season (March to August)), and the mobbing assemblage size. In addition to phylogeny, we included in both models the location and the date of each trial as a random effect to control for repeated sampling in the same location. For these models we included all 79 species that mobbed at least once.

We used the package 'car' (Fox and Weisberg 2011), to test for collinearity using the generalized variance inflation factor (GVIF) (Appendix S2), which revealed that the factors in our models have a low collinearity (all GVIFs are smaller than 1.32). We tested specific hypotheses based on our *a priori* predictions and thus only the terms that represent these hypotheses were

254 included and non-significant terms were retained in the models. We note that
255 the inclusion of the non-significant terms did not influence the qualitative
256 interpretation or significance of the other parameters.
257
258 **Results**
259 We observed 157 bird species in the study area (Appendix S2), of which 79
260 species (50.31%) mobbed in at least one of the experiments. Overall, 26
261 species mobbed both models, 50 species only mobbed the high-risk model
262 (Ferruginous Pygmy-Owl), while three species only mobbed the low-risk model
263 (Burrowing Owl).
264
265 Bird species with smaller body mass were more likely to mob (table 2, figure
266 1a). Species that forage in the understory or canopy were more likely to mob
267 than species that forage on the ground (table 2, figure 1b). Moreover, species
268 that flock or live in stable groups were more likely to mob than solitary species
269 (table 2, figure 1c). The social system did not influence whether species
270 engaged in mobbing (table 2). Also, the relative abundance of a species
271 (encounter rate) did not influence whether it engaging in mobbing (table 2).
272
273 Birds adjusted their mobbing behavior depending on the risk posed by a
274 predator. The mobbing assemblage was larger when birds mobbed the high-
275 risk predator model than the low-risk one (table 3, figure 2), but mobbing
276 intensity and the mean body mass of species that mobbed did not influence the
277 number of individuals in a mobbing assemblage (table 3). Furthermore, birds

278 mobbed more intensively when mobbing the model of a low-risk predator than
279 the high-risk one (figure 3), and individuals of smaller species mobbed more
280 intensively than individuals of larger species (table 4).
281
282 **Discussion**
283 Our results revealed that particularly species that are potential prey engage in
284 mobbing, but only if they can afford to do so. Accordingly, ground-living species
285 that experience the highest risk of being killed by perch-hunting owls, and
286 solitary species that cannot benefit from safety in numbers, were less likely to
287 mob. In contrast, species that utilize safer parts of the habitat (understory or
288 canopy), and species that benefit from safety in numbers, were more likely to
289 engage in mobbing. Species that engaged in mobbing adjusted their behavior
290 depending on the risk posed by the predator. In the presence of the high-risk
291 predator, larger mobbing assemblages formed, but individuals took less risks
292 than in the presence of a low-risk predator, confirming findings from previous
293 studies (Maloney and McLean 1995; Veen et al. 2000; Griesser 2009).
294
295 *Size matters hypothesis*
296 It has been suggested that potential prey particularly mob predators (Hartley
297 1950; Dutour et al. 2016), but this hypothesis has so far not been tested across
298 species. Our results lend support to this hypothesis, showing that species that
299 engage in mobbing are lighter than species that do not mob, and thus, are
300 within the prey body-size range of the two owl species (i.e., weigh less than
301 200g (Motta-Junior 2006; Carrera et al. 2008)).

302

303 *Safer niche hypothesis*

304 In support of this hypothesis, terrestrial species were less likely to mob than
305 understory or canopy-living species. The owl models used in this study are
306 perch-hunters that attack with a top-down strike, and consequently, terrestrial
307 species are under the highest risk (Lima and Dill 1990; Kullberg and Ekman
308 2000; Hedenstrom 2001). Accordingly, they may have evolved alternative
309 strategies of dealing with perched predators, for example by relying on
310 camouflage as found in tinamous (Tinamidae) and nightjars (Caprimulgidae).
311 The predation risk should not only vary depending on the strata, but also across
312 different habitats. Since our experiments were conducted in one habitat type
313 only (i.e., relatively open areas at the edge of forest patches), we cannot test
314 this hypothesis. A study on powerful owls *Ninox strenua* showed that they were
315 equally likely to roost in forest patches and in open areas (Pavey and Smyth
316 1998). However, owls were more frequently mobbed in open habitats during
317 daytime roosting (i.e., their typical hunting area at night), indicating that prey
318 adjust their mobbing behavior depending on habitat-specific risks.

319

320 *Safety in numbers hypothesis*

321 A number of studies demonstrated that being in a larger group dilutes the risk
322 to an individual (Hamilton 1971), and reduces the probability of a successful
323 predator attack due to the confusion effect (Miller 1922). In support of this idea,
324 our results showed that gregarious species that join flocks or live in stable
325 groups are more likely to mob than solitary species (table 1). Thus, even though

326 solitary species could benefit from safety in numbers in a heterospecific mob,
327 they still do not mob. This finding suggests that solitary species may have
328 evolved different strategies of dealing with predators as discussed above, but
329 further studies are required to explore this idea.
330
331 *Social system hypothesis*
332 Previous studies in a family-living bird species showed that parents mob more
333 intensively in the presence of independent offspring (Griesser and Ekman
334 2005), and that mobbing provides a social learning opportunity to learn to
335 recognize predators (Griesser and Suzuki 2017). In contrast to our prediction,
336 the social system of a species did not influence their likelihood to engage in
337 mobbing. Clearly, predator mobbing can have social functions also in non-
338 family living species, such as providing opportunities to recruit partners for
339 future mobbing events (Krams et al. 2008), to form dispersal coalitions
340 (Maklakov 2002), or to display their quality to potential mates (Cunha et al.
341 2017a).
342
343 *Mobbing plasticity depending on the risk*
344 Previous studies showed that birds recognize their predators (Curio et al.
345 1978b; Griesser and Ekman 2005), and adjust their behavior depending on the
346 specific risks that a predator poses (Griesser 2009; Motta-Junior and Santos-
347 Filho 2012; Tvardíková and Fuchs 2012). In accordance, our findings show that
348 birds mob less intensely but form bigger assemblages when mobbing a high-
349 risk predator compared to a low-risk predator. A previous study reported that

350 Neotropical birds mobbed a dangerous predator (i.e., striped owl *Asio stygius*)
351 more intensely than a less dangerous predator (i.e., barn owl *Tyto alba*) (Motta-
352 Junior and Santos-Filho 2012). However, these species not only have very
353 different diets, but they are also morphologically distinct and are
354 crepuscular/nocturnal, which may influence the mobbing response of birds. In
355 contrast, we used predator species that are morphologically similar and have
356 diurnal habits. Diurnal owls are a constant threat to most diurnal bird species,
357 therefore the risk of mob a potential threating predator at daytime may be higher
358 than a nocturnal one, which does not impose an immediate threat. Thus, it may
359 be less costly to approach high-risk nocturnal predator than a diurnal high-risk
360 predators. Moreover, the similar plumage of the owls species excludes the
361 possibility that differences in the mobbing behavior were caused by body
362 coloration.
363
364 We did not find a difference in the mobbing behavior (intensity and assemblage
365 size) across seasons (breeding *vs*. non-breeding). Similarly, a study with
366 drongos (*Dicrurus macrocercus* and *D. leucophaeus*) showed that there was
367 no difference in the frequency that birds mobbed their predators between
368 different seasons (Nijman 2004). Birds may adjust their mobbing behavior
369 according to the season particularly in a nest defense context (Shedd 1992;
370 Shedd 193). We used predators of adults as stimuli, which pose a risk
371 independent of the season. Moreover, some bird species are year-round
372 territorial, and territoriality seems to influence aggressive behavior (Haul et al.

373 2004) and may also influence mobbing behavior, principally during the non-
374 breeding season.
375
376 **Conclusions**
377 Animals can only die once, and thus, prey should adjust their behavior to
378 minimize the risk of immediate death, for example during predator mobbing.
379 Mobbing and other anti-predator behaviors generally are studied from the
380 perspective of those that display it. However, to fully understand factors that
381 facilitate the evolution of these behaviors, it is important to compare species
382 that display these behaviors with those that do not display it. Our results show
383 that only species that can afford mobbing, and do not pay too high costs,
384 express this behavior. Clearly, mobbing is only beneficial for species that can
385 be killed by a given predator.
386 Recent studies showed that predator mobbing also has important social
387 functions, such as learning to recognize predators (Griesser and Suzuki 2017),
388 to advertising their phenotypic quality to potential mates (Cunha et al. 2017a),
389 learning to recognize alarm calls of heterospecifics (Templeton and Greene
390 2007), and enhancing social bonds (Krams et al. 2008). Thus, mobbing can
391 encompass a range of functions, calling for empirical studies that quantitatively
392 assess the energetic costs and fitness benefits of mobbing across species,
393 further contributing to the understanding of the evolution of risk taking
394 behaviors.

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612 **Figure 1. 1a)** Probability of species mob at least one of the two owl models
613 according to the body mass of bird species. Graph based on predicted values
614 from the generalized mixed model using MCMCglmm, the grey area indicates
615 the 95% credible interval. The empty circles are the predict values, while the
616 ticks are the raw values. 1b) Probability of species mob at least one of the owl
617 models according to the foraging strata that each species occupy. Graph based
618 on predicted values from the generalized mixed model using MCMCglmm. 1c)
619 Probability of species mob at least one of the owl models according to the
620 foraging strata that they occupy. Graph based on predicted values from the
621 generalized mixed model using MCMCglmm.
622
623 **Figure 2.** Number of individuals in the mobbing assemblage according to the
624 risk represented by the predator stimuli (high-risk, low-risk). Graphs are based
625 on raw data, bars indicate 95% confidence interval.
626
627 **Figure 3.** Mobbing intensity according to the risk represented by the predator
628 stimuli (high-risk, low-risk). Graphs are based on raw data, bars indicate 95%
629 confidence interval.
630

631

632 **Table 1.** Phylogenetically controlled generalized linear mixed model, using
633 MCMCglmm, comparing the effect of body mass (logarithmic scale - g),
634 foraging strata (ground, understory or canopy), flocking behavior (yes or no),
635 and social organization (non-family/cooperative, family living, cooperative), the
636 encounter frequency rate (encounter per min) on the propensity of species to
637 mob or not mob predators. Significant P-values are highlighted in bold.

	estimate	95% CI		pMCMC
		lower	upper	
intercept	2.87	-0.73	6.02	0.11
body mass*	**-2.04**	**-2.75**	**-1.22**	**< 0.001**
foraging strata (ground vs. canopy) †	**3.40**	**0.87**	**5.83**	**< 0.001**
foraging strata (ground vs. understory) †	**2.66**	**0.46**	**4.96**	**0.010**
flocking behavior (no vs. yes) †	**1.83**	**0.58**	**3.00**	**0.006**
social organization (non-family vs. family) †	0.71	-0.79	1.93	0.30
social organization (non-family vs. coop.) †	1.08	-1.66	4.08	0.49
encounter frequency rate (encounter/min)	-11.15	-36.03	14.34	0.40
random effects				
phylogeny	1.03	0.74	1.30	

638 †Reference level is the first category in these lists.

639 **Table 2.** Phylogenetically controlled generalized linear mixed model, using
640 MCMCglmm, comparing the effect of risk posed by a predator, mobbing
641 intensity, season and body mass on the mobbing assemblage size. Significant
642 P values are highlighted in bold.

	estimate	95% CI		pMCMC
		lower	upper	
intercept	**0.99**	**0.58**	**1.31**	**<0.001**
predator model (high-risk/low-risk)†	**0.35**	**0.04**	**0.68**	**0.034**
mobbing intensity	-0.00	-0.02	0.02	0.76
season (non-breeding/breeding)†	-0.15	-0.45	0.13	0.30
body mass	-0.00	-0.05	0.04	0.90
random effects				
phylogeny	0.005	0.001	0.01	
location	0.49	0.33	0.67	
date	0.03	0.00	0.09	

643 † Reference level is the first category in these lists.

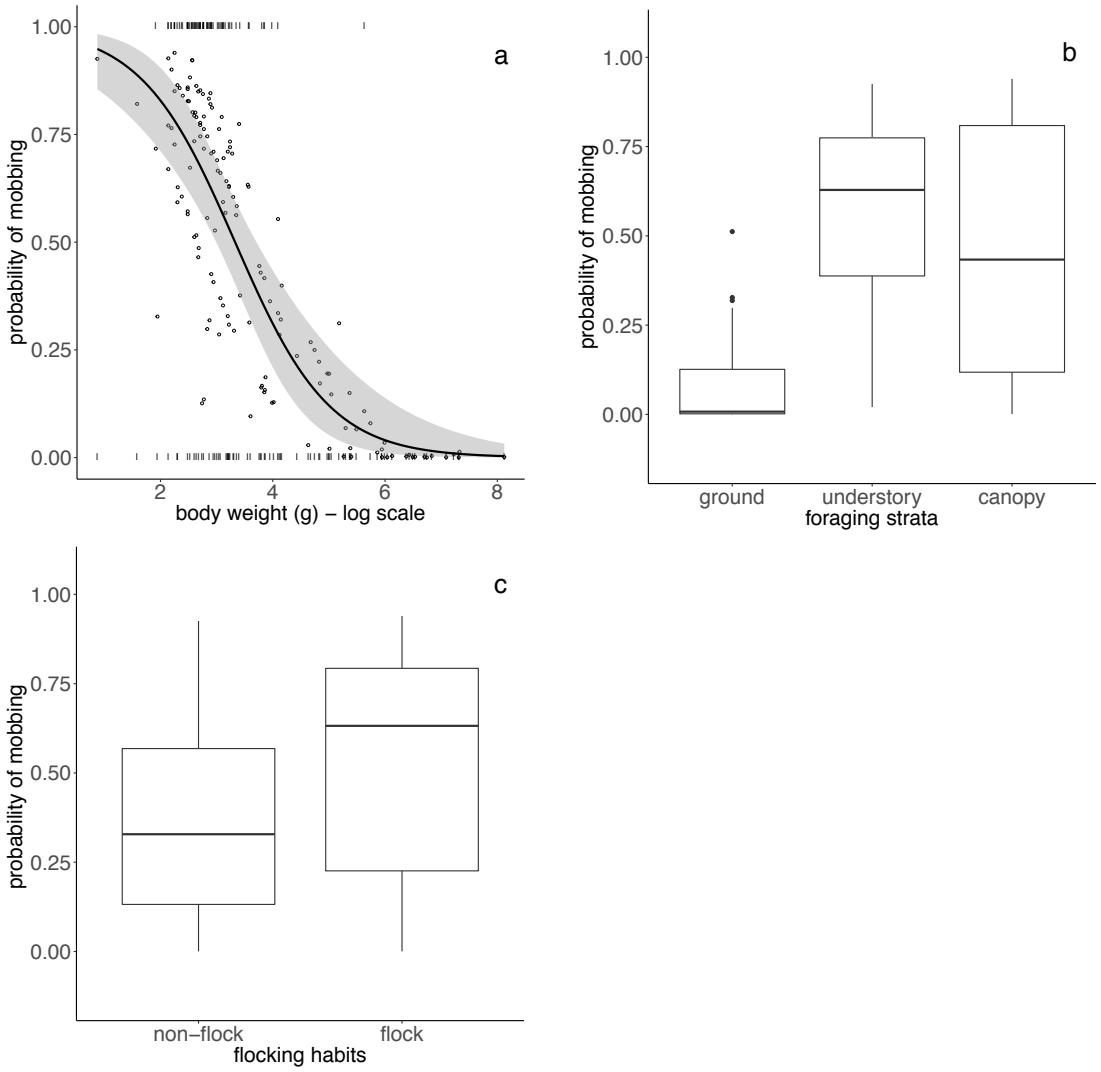
644 **Table 3.** Phylogenetically controlled generalized linear mixed model, using
645 Markov chain Monte Carlo technique, comparing the effect of risk posed by a
646 predator, mobbing assemblage size, season and body mass on the mobbing
647 intensity. Significant P values are highlighted in bold.

	estimate	95% CI		pMCMC
		lower	upper	
intercept	**2.10**	**0.93**	**3.21**	**<0.001**
predator model (high-risk/low-risk)†	**-0.75**	**-1.39**	**-0.09**	**0.026**
mobbing assemblage	-0.01	-0.04	0.08	0.62
season (non-breeding/breeding)†	-0.08	-0.88	0.78	0.83
body mass	**-0.004**	**-0.008**	**-0.0006**	**0.032**
random effects				
phylogeny	1.00	0.97	1.02	
location	1.00	0.97	1.03	
date	0.99	0.97	1.02	

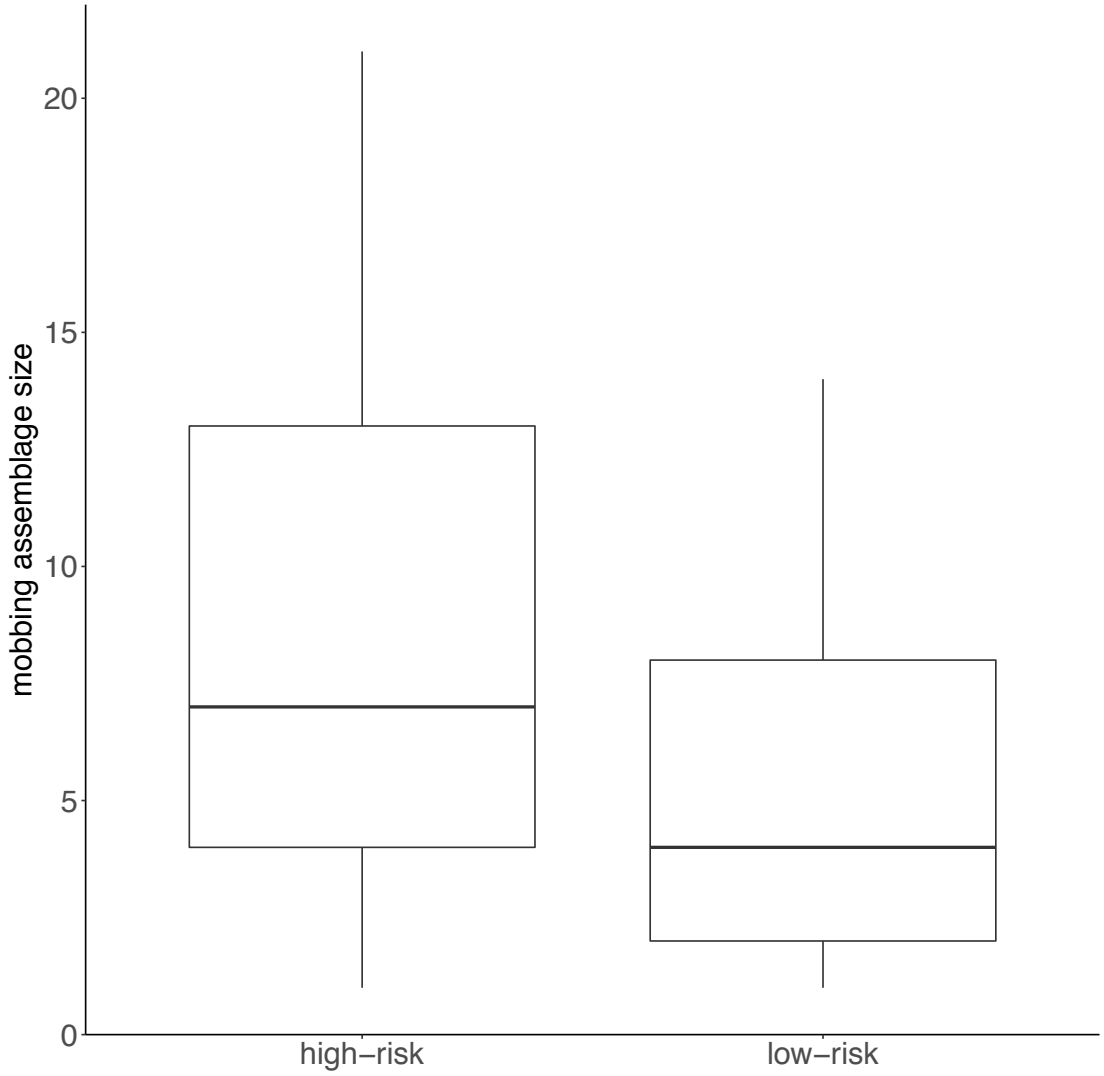
648 † Reference level is the first category in these lists.

649

Figure 1. 1a) Probability of species mob at least one of the two owl models according to the body mass of bird species. The grey area indicate the 95% credible interval. The empty circles are the predict values, while the ticks are the raw values. 1b) Probability of species mob at least one of the owl models according with the foraging strata that each species occupy. 1c) Probability of species mob at least one of the owl models according with the foraging strata that they occupy. All graphs based on predicted values from the generalized mixed model using MCMCglmm.



662 **Figure 2.** Number of individuals in the mobbing assemblage according to the
663 risk represented by the predator stimuli (high-risk, low-risk). Graphs are based
664 on raw data, bars indicate 95% confidence interval.



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667 **Figure 3.** Mobbing intensity according to the risk represented by the predator
668 stimuli (high-risk, low-risk). Graphs are based on raw data, bars indicate 95%
669 confidence interval.
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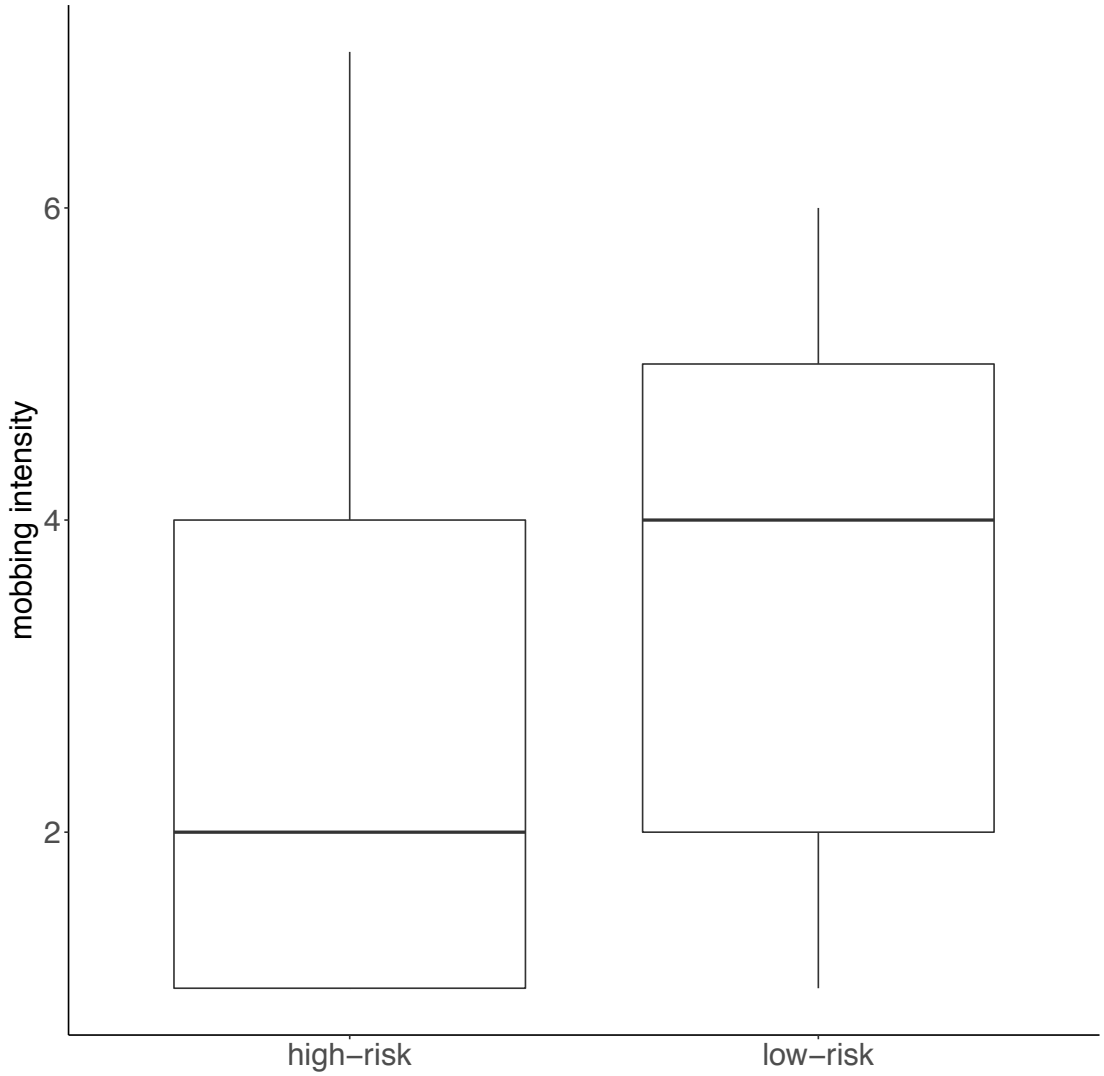

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